*THE PROGRESS AND PROBLEMS OF PLANT PHYSIOLOGY.**

THERE are some subjects of whose content and extent most educated people have fairly accurate conceptions, though they may not appreciate the significance of the numerous problems which those who carry forward research are attacking. Literature and history number their appreciative amateurs by thousands. Even such sciences as astronomy and chemistry receive a fair measure of popular approbation and are widely appreciated.

Unhappily this is not yet the case with botany. By even the limited number who think they know of what it treats, it is frequently misunderstood and consequently undervalued. To most mature people it is hardly more than a name for a dilettantish dissecting of flowers, for which an apprenticeship of memorizing troublesome technical terms must needs be served.

It is easy to discover why this is so. It has resulted from the mistaken ways of presenting the subject to elementary pupils. But the difficulty of correcting the misapprehension is not decreased by a knowledge of the way in which it has arisen. We can only rely upon the gradual substitution of better ideas in the newer generation by means of more adequate instruction, and on the occasional popular presentation of more accurate information. For the former we may look to the schools, which are rapidly changing the scope of their teachings. The latter, however, should be undertaken by specialists, as a matter both of duty and of privilege. Popular accounts of plant phenomena may be accurate without being dull, interesting without being sensational, and attractive without being sentimental. But we can expect these characteristics only in properly qualified writers whose scientific training has been sufficient to kindle their enthusiasms and quicken their energies—without spoiling their English. Such books, in considerable number, have been appearing lately from American writers. May their tribe increase! As books of this kind are multiplied we may hope for an increasing appreciation of the science of botany both educationally and economically.

When the general subject has been so misapprehended, what can be expected regarding one division of it? The experimental study of the physiology of plants is not new. Hales more than a century ago carried out such accurate experiments that they are quoted to-day. But even to fairly-educated people the word physiology, conjoined with plant, conveys no definite idea. 'Physiology' we studied at school; is it not that hybrid of human anatomy and hygiene, with barely enough real physiology to salt it, which is inflicted upon immature youngsters, to the accompaniment of lurid lithographs of an inebriate's stomach? But what can 'physiology' have to do with plants that have no teeth to decay, stomachs to ulcerate, or eyes to become myopic? And so it comes about that one must explain to the average man that plants are really alive, that they work and rest, that they are sensitive to what goes on around them, and that they have established relations with their plant and animal neighbors. How they do these things and how their activities underlie those of all other living beings, even man's, lies within the compass of this branch of the science of botany.

But to such a company as this it is not necessary to set forth in detail the province of plant physiology or to justify its rapid introduction into institutions of higher learning. While Cæsalpino and the schoolmen argued vainly about the location of the 'soul' of plants, it was the growing

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dissatisfaction with the empty reasonings of such scholastic philosophy that drove men to observe the phenomena of nature. Thus real physiology had its birth in the last half of the seventeenth century, only a little later than the other natural sciences. It is, however, only in comparatively recent years that plant physiology has become established upon a firm experimental basis and thus fitted to take its proper place among the sciences offered in university curricula. Its real and vigorous growth has been measured by scarcely four decades. Among the countless results of the rejuvenation of biology wrought by various cooperating causes about the year 1860, may be enumerated the rise of plant physiology. One of the first evidences of this renascence was the publication in 1865 of Sachs's *Handbuch der Experimental-Physiologie*, the first volume which gave any comprehensive and clear view of the phenomena of plant life.

From that day to this, with increasing vigor, Sachs's countrymen have been prosecuting researches into plant doings and guiding many students in their maiden investigations. French, Austrian, Italian and Russian students have also made notable advances. On the continent a few great centers of physiological research have been developed, like Würzburg, Tübingen, Leipzig, Bonn, Berlin, Vienna, Prag and Paris. Great Britain has made a notable beginning at three of her great university centers.

But in this country the specialization which alone makes possible the effective development of a subject, has been slower in coming, and it is scarcely a decade since physiology began to have any considerable attention. Five years ago (I speak by the card) one could count on the fingers of one hand the colleges which offered any but brief lecture courses in plant physiology, and the number giving even lecture courses was less than 4% of the total number of colleges. I am sure that many in this audience would be surprised were I to recite the long list of prominent institutions which gave no physiological courses—*some even no botany*. In late years many have made a beginning in the way of demonstration and lecture courses, but the number with even fairly equipped physiological laboratories is still few. Indeed, there are to-day not twenty-five institutions of higher learning in the United States which offer laboratory instruction in plant physiology, even in an elementary way, and still fewer which give opportunity for as much as a year's work. Graduate work in physiology, if the Graduate Handbook for 1898–9 may be relied upon, is now offered only at Barnard, Chicago, Columbia, Harvard, Michigan, Minnesota and Pennsylvania.

The development of centers of physiological research is therefore a matter of the future. It cannot be long delayed, however, for there is noteworthy energy in the advancement of this subject in several of the stronger institutions.

To the professional botanists, who are especially concerned in the advancement of the science, it would doubtless be of some interest should I take this opportunity to recapitulate the investigations which have been most fruitful of progress in the past decade. But the field is so vast, and work is being so vigorously prosecuted, that I should despair of being able, within the limits custom sets, to present adequately the march of our knowledge of plants within the last decade. To such a task, moreover, my own knowledge would be wholly inadequate.

Therefore, instead of presenting a summary of so extensive an investigation, I choose rather to confine my attention to the physiological aspects of botany, and in this field to endeavor to bring before you a conception of the general *trend* of investigation, without any endeavor to mention the work of individuals or even the important isolated

researches which may be the starting points of new lines of progress. At the same time I shall seek to indicate what I conceive to be fruitful lines of study and shall direct attention to some of the unsolved problems which still confront the physiologist.

PHYSICAL CHEMISTRY.

The physiologist is dealing with material phenomena as manifested by living things. Physiology is, therefore, chiefly the application of the knowledge of chemistry and physics to the phenomena of life. It follows that the physiologist must be familiar with the laws deduced by chemists and physicists from their study of matter which is not under the influence of life. He needs to be equipped with the best physical and chemical knowledge of the day. Because of a want of such training reproach has often fallen upon physiology in the past. Inattention to these underlying sciences has led to divers fantastic explanations of phenomena—explanations forbidden by the fundamental facts of chemistry and physics. Compelled thus to rely on advance in other sciences for the possibility of progress in their own, physiologists welcome with the brightest anticipations the rapid growth and development of that field in which chemistry and physics merge—physical chemistry. There is much, it is true, with which its students concern themselves that does not touch directly the activities of plants. But some of its subjects are of the most intimate concern to physiologists.

Solutions.—This is notably the case with the comparatively recent coordination of long known facts and late discoveries into clear and definite laws of solutions. In no condition, outside and inside the plant body, does matter play a more important physiological rôle than in a state of solution in water. The prevalence of a cellulose wall, jacketing the protoplasm of their cells, is probably the most characteristic mark of plants. This membrane precludes the entrance into the body of any substance not in solution, whether originally solid or gaseous. Thus the behavior of solutions is of fundamental importance for the absorption of foods by the colorless plants and of the raw materials out of which the green plants can make foods.

The cellulose wall has been adapted by plants to subserve a function unknown in the animal body, namely, turgor. Only a knowledge of solutions enables us in a measure to understand the existence and regulation of turgor. The solutions enclosed by the semipermeable protoplasmic membrane of the living cell are rarely or never the same as those outside the plant or in paths of water conduction. Such a condition establishes at once a movement of water into the cell and develops a definite amount of hydrostatic pressure, equivalent to the osmotic pressure of the dissolved substances. Thus, by a figure, it is said that the osmotic pressure of the internal solutions pushes outward the protoplasm, backed by resistant but elastic wall, which stretches until its elastic resistance balances the osmotic pressure. If the cell be one of a group the cohesion and turgidity of the cells surrounding any one resist its enlargement. Thus all the cells of a turgid mass of tissue bear firmly against one another, and this condition is of great importance in maintaining the form of young parts in which as yet no mechanical tissues exist. Turgor has its influence also in regulating the diffusion of water vapor through the stomata, in transfusing liquid water through water glands, in certain forms of secretion, and so on. So important is turgor that special salts seem to be provided to maintain it at a normal point. Its relations to growth also are unquestionably of prime importance, but we are not able at present to interpret these relations satisfactorily. Although the statement is

generally made that turgidity is a prerequisite for growth and regulates it, there are some strong reasons for thinking that the relation is rather the reverse, and that growth regulates turgor.

Pathological changes may also be brought about by abnormally high osmotic pressure, a notable instance being furnished by œdema of various organs, especially leaves. In such a case, turgor seems to distend the cell walls extraordinarily, and to act as a stimulus on growth, causing a local hypertrophy characterized by bladdery tissues.

For interpreting all these processes, most fundamental for nutrition and growth, the new knowledge of solutions furnishes invaluable aid. This theory, developed mainly within the last decade by the labors of Pfeffer, Van t'Hoff, Arrhenius, Ostwald, Raoult, and others, looks upon a substance in solution in water as essentially a gas. Its molecules are freer to move than they are in the solid state because of their relations to the molecules of water. These, at the same time that they make mobility possible, obstruct the movements of the solute, so that the molecules of the latter are not nearly so free to move as the molecules of a gas. Thus enormous pressures are necessary to move the solute through the solvent or to remove its molecules from it. Many demonstrations establish firmly the fact that the molecules of solutes exhibit the well-known laws of gases. This general applicability of the fundamental laws of gases to solutes has made evident the proper basis of comparison between solutions of different compounds. For many years, and for some years after a proper knowledge of physical chemistry would have led to their abandonment as not comparable, physiologists were comparing the physiological action of percentage solutions or solutions of definite specific gravity, in ignorance that this was like comparing the action of one gas at atmospheric pressure with that of another at 10 atmospheres pressure. Henceforth, we must deal with equi-molecular solutions if a comparative knowledge of physiological action is sought.

A further study of the behavior of solutions has made us acquainted with the fact that when water solutions which conduct electricity, *i. e.*, electrolytes, are of less than a certain concentration, the solute undergoes partial dissociation, no longer existing alone as a definite chemical compound. A certain amount, depending on the concentration of the solution, is broken up into electrically charged part molecules or ions, which behave osmotically as molecules and increase the osmotic pressure of the solute. Moreover these ions exert a very marked physiological effect upon the protoplasm. Certain ions are extremely injurious, inhibiting the activity of the protoplasm and resulting in death. Poisons, so called, produce a similar result. It is possible that by a study of ionic action we may obtain a more accurate idea of what actually happens when living matter dies by 'poison.' It would be surprising were there not a considerable diversity in the actual effects of various 'poisonous' agents.

Again, certain ions have a less marked physiological action, which is designated as stimulation, calling forth corresponding change in the activity of the protoplasm. Unquestionably many of the peculiarities of growth and development of an organism are responses to the action of ionic stimuli, but of these practically nothing is yet known. Certain human sensations have already been shown by Kahlenberg in his investigations on taste to be due solely to the action of definite H and OH ions. In no organisms is there so good an opportunity as among plants to determine precisely how these factors, always acting in complex combinations, effect the modifications of form and function that constitute adaptation to external conditions.

Studies of this kind have barely begun. Kahlenberg and True were the first to establish the poisonous action of ionic hydrogen in solutions of certain acids and salts. A few other observers have attacked similar problems, but the field is hardly yet explored ; it has not been at all cultivated. The relations are complex, it is true, and their unraveling will not be easy; but surely there are rich harvests for the patient worker.

In the light of the modern theory of solutions, it is essential that the whole field of root absorption be reexamined. Dilute solutions of the soil must surely be electrolytically dissociated in large measure, and this fact doubtless stands in intimate relation to the entrance of solutes into the plant. In the absence, at present, of complete experimental demonstration of the behavior of these substances, we are compelled to rely largely upon theoretical probabilities. Interesting possibilities, however, present themselves to the speculative worker and point out various directions in which investigation may be fruitful.

Energy.—One of the directions in which physical knowledge is now extending, but in which it is still so imperfect as to leave much to be desired, is in the understanding of the forms and transformations of energy. But the physiology of plants has not yet made use of all the knowledge that is available in this direction. Though in the past decade we have had some important researches, there yet remain great gaps in our knowledge of the income of energy to the plant and of the ways in which it is utilized. I may here indicate only a few of these gaps in our knowledge.

While it is easy to calculate the potential energy of the foods absorbed it is not easy to determine how much of the energy is available, in what form it is released and what changes it undergoes, as it is used by the plant.

We know that heat is one form of energy which is constantly affecting the organism, and we speak of certain temperature limits as one of the essential conditions for life. But what does that mean? Why is it a condition of life? Is it merely because the necessary chemical changes can only occur within certain limits? If so, what does *this* mean? Does it mean that the radiant energy which imparts to us the sensation of heat must be acting upon the molecules of the various chemical compounds ere they are capable of enough lability to afford the living protoplasm opportunity to push them over, so that they fall into simpler compounds, or to lift them to a higher level of complexity and to greater instability? If heat does not merely increase chemical instability, is life possible within certain limits of temperature because there is pouring into the organism a supply of energy which the protoplasm may utilize in directer fashion to do the work necessary to existence?

What is the source of energy for the colorless plants which assimilate the simpler foods? It is almost inconceivable that they can produce proteids out of the carbohydrate and nitrogen compounds with which they can be supplied without needing a considerable amount of energy besides the potential energy which reaches them in the foods they absorb. If there is no direct supply of radiant energy, it looks very much as though these plants had acquired the long-sought power of lifting themselves by their own boot straps. Yet if radiant energy, either as light or heat, is utilized by them, we know nothing of it at present. Or is it the energy of the O_2 absorbed for respiration which accounts for the extra work done? The data are not at hand to determine the correct answer to these questions. General statements abound, and to many it may seem that all this is known, since it is often dogmatically settled in text-books. Yet in reality we must have

exact measurements of the amounts of energy involved—a thing not yet accomplished—before we can be said really to know whence plants derive their energy and what heat means for them.

Even the case of the green plants is not at all clear. That they construct their own food in great measure is certainly true. That they do this by using absorbed radiant energy of the quality which gives us the sensation *light* is well known. But it is by no means clear, in terms of chemistry and physics, how this is done, or even what measure of the absorbed energy is utilized. Measurement, indeed, is difficult, yet quantitative results are necessary before we can be satisfied that we know what is happening when the leaf makes food.

Finally it may be said that little is yet known of the energy relations in the processes of growth. Here, since we must deal wholly with internal release and utilization of energy, investigation will be most difficult and uncertain.

Stereochemistry.—The decade that is passing has witnessed the very great extension of chemical knowledge in the direction of the constitution of the molecules of carbon compounds. Stereochemistry touches plant life most obviously in its relation to the carbohydrates, which are constructed by the green plants, and digested and utilized by all. The phenomenal work of Fischer on the sugars, supplemented as it has been by that of Tollens, Kiliani, Lobry de Bruyn and others on asymmetric carbon atoms, has put us in possession of facts which throw a flood of light upon nutrition and are destined when more completely exploited and fully applied, to elucidate many difficulties in our present thinking about the feeding of plants.

We have learned for example that a carbon compound, to be a valuable food, must not only contain C, H and O, but that these must be combined in a particular fashion. The aldehyde group CHO, the ketone group CO, and the radical CH_2OH are characteristic of good foods. The simpler sugars such as glycerose and arabinose; the hexoses, glucose or grape sugar, fructose, or fruit sugar, mannose and galactose; the polysaccharides, sucrose or cane sugar, lactose or milk sugar, and maltose or malt sugar are all substances which have been proved useful as plant foods, and all contain one or more of these groups.

Up to a certain limit, the presence of a particular molecular group increases the food value. What does this phrase 'food value' mean? Does food value depend solely on availability of energy, *i. e.*, the ease with which it can be released? Or has the form in which energy is set free something to do with its availability and the consequent food value? Or does the constitution of the molecules before and after decomposition affect food value? If so, is it because the constitution of the molecules is related to the form in which energy is released or because it is related to the ease with which energy is released?

When the complex carbohydrates like starch and inulin are to be utilized, they break down through a series of dextrins and levulins respectively, finally becoming simplified to hexose sugars. Why is this necessary? And how are we to interpret these decompositions? Are they part of the energy-release? It can hardly be doubted that the constitution of the molecules of starch and inulin, composed as they are of units of glucose and fructose, determines the permanence while in the storage form, and that separation into their constituent units in digestion makes possible the assimilation of the sugars as food. It is plain, therefore, that a precise knowledge of the constitution of starch and inulin is a desideratum. We must look forward also to further extension of stereochemical knowledge of the almost infinite variety of

the other carbon compounds and to the investigation of the nitrogenous substances, as yet scarcely well begun. These may be expected to put physiologists into possession of valuable clues to the secrets of nutrition and respiration.

How intimate this relation between the arrangement of atoms in space and physiological activity is, is to be seen in the fact that fermentability is dependent upon the configuration of the sugar molecule. It has been found that, of the many sugars known, only those with 3, 6, or 9 atoms of carbon in the molecules are fermentable. Thus the triose sugar, glycerose, whose formula is $C_3H_6O_3$, is fermentable, while the tetrose sugar, erythrose, $C_4H_8O_4$, and the pentoses, ribose, lyxose, xylose, and arabinose, $C_5H_{10}O_5$, are not. In like manner several of the hexoses, $C_6H_{12}O_6$, and the nonnoses, $C_9H_{18}O_9$, are fermentable, while the intermediate ones, such as the heptoses, $C_7H_{14}O_7$, are not.

But the relation is yet more intimate. Even when the proper number of atoms is present they may be arranged in such a fashion as not to be open to disturbance by an organism.

Thus, certain species of yeast are capable of fermenting *d*-glucose, *d*-mannose, and *d*-galactose. The arrangement of their molecules may be represented in a plane as follows:

$$d\text{-glucose} = \begin{array}{ccccccccccc} & & \mathrm{H} & & \mathrm{H} & & \mathrm{OH} & & \mathrm{H} & & \\ \mathrm{CH_2OH} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{COH} \\ & & \mathrm{OH} & & \mathrm{OH} & & \mathrm{H} & & \mathrm{OH} & & \end{array}$$

$$d\text{-mannose} = \begin{array}{ccccccccccc} & & \mathrm{H} & & \mathrm{H} & & \mathrm{OH} & & \mathrm{OH} & & \\ \mathrm{CH_2OH} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{COH} \\ & & \mathrm{OH} & & \mathrm{OH} & & \mathrm{H} & & \mathrm{H} & & \end{array}$$

$$d\text{-galactose} = \begin{array}{ccccccccccc} & & \mathrm{H} & & \mathrm{OH} & & \mathrm{OH} & & \mathrm{H} & & \\ \mathrm{CH_2OH} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{COH} \\ & & \mathrm{OH} & & \mathrm{H} & & \mathrm{H} & & \mathrm{OH} & & \end{array}$$

But *d*-talose, whose structure is the following:

$$\begin{array}{ccccccccccc} & & \mathrm{H} & & \mathrm{OH} & & \mathrm{OH} & & \mathrm{OH} & & \\ \mathrm{CH_2OH} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{COH} \\ & & \mathrm{OH} & & \mathrm{H} & & \mathrm{H} & & \mathrm{H} & & \end{array}$$

cannot be fermented by these yeasts. Inspection shows that *d*-talose differs from *d*-galactose and *d*-mannose only in the transposition of the molecular groups about a single one of the asymmetric carbon atoms, and from *d*-glucose only in the transposition about two carbon atoms.

Again, while *d*-glucose,

$$\begin{array}{ccccccccccc} & & \mathrm{H} & & \mathrm{H} & & \mathrm{OH} & & \mathrm{H} & & \\ \mathrm{CH_2OH} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{COH,} \\ & & \mathrm{OH} & & \mathrm{OH} & & \mathrm{H} & & \mathrm{OH} & & \end{array}$$

is fermentable, its isomer, *l*-galactose

$$\begin{array}{ccccccccccc} & & \mathrm{OH} & & \mathrm{OH} & & \mathrm{H} & & \mathrm{OH} & & \\ \mathrm{CH_2OH} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{C} & — & \mathrm{COH,} \\ & & \mathrm{H} & & \mathrm{H} & & \mathrm{OH} & & \mathrm{H} & & \end{array}$$

is not at all fermentable.

The discovery that yeasts, long believed to show direct ferment action of the protoplasm, produce the chemical changes known as fermentation by the intervention of enzymes, removes the problem from the immediate field of physiology, only to group it with the host of baffling catalytic phenomena which the chemist is at present wholly unable to explain. Thus all fermentations at present known become closely associated with the digestive processes in nutrition. We may scarcely expect light upon all these phenomena until the preparation of the enzymes in a state of purity is attained. This, it is to be hoped, will be followed by a knowledge of their composition, though, as they now appear to belong to the group of nucleo-proteids, this may only be ascertained when the long-awaited desideratum is attained and we know the composition of proteids themselves.

The action of the enzymes, which is limited by the molecular constitution of the substances they hydrolyze and break up, is

probably dependent upon their own constitution. Fischer's researches seem to show that the molecular relation between the two are as intimate as those between a key and the lock whose wards it must fit before the position of the parts can be altered. If this proves to be true, we shall look for a better understanding of the processes of digestion with the further extension of the stereochemistry of the nitrogen compounds.

Again a knowledge of the physiological action of definite radicles, which may differ according to their position in the molecule, is being reached by determining the effect of the introduction of a certain radicle or of a change in its position. The ability to alter chemical structure at will by known reactions puts it into our power to ascertain how each change affects the protoplasm. Thus in the phenols, a series of compounds allied to the tertiary alcohols, of which the so-called 'carbolic acid' is a familiar example, True and Hunkel find that the introduction of the nitro group (NO_2) or the methyl group (CH_3) into the benzene nucleus increases the poisonous effect, while an increase in the number of hydroxyl groups (OH) or nitro groups (NO_2) has little or no effect.

PHYSIOLOGICAL MORPHOLOGY.

Within the past decade attention has been especially directed to the causes which affect the development of plants and determine both form and structure. A moment's thought suffices to impress upon any one the fact that a great number and extreme variety of external agents are acting and interacting in most complex fashion upon all plants. Some of the more obvious of these groups of external causes are even popularly recognized. Thus one hears it said that poor soil and scanty water is the cause of the dwarfing of plants, which under better conditions attain a greater stature.

Such apparently obvious deductions may be correct, or may not be, but satisfactory and accurate analysis of the effects of external agents is a problem of the utmost difficulty, because it is well-nigh impossible to alter experimentally one condition without really altering others at the same time. The solution of the problems of physiological morphology is, therefore, only to be attained by the most assiduous care in experiment and induction.

Morphology.—In illustration of these problems I may refer to the recent studies made by Klebs on the external factors which control various reproductive processes among the algæ. By experimental analysis he has sought to determine the bearing of light, temperature, density of medium, and various other agents upon the production of zoospores and gametes. These studies have shown that it is possible to call forth a definite and very complicated physiological process, of far-reaching consequences, by appropriate changes in the environment. How they operate remains yet to be explained.

In the higher plants the investigations of Goebel and many others have shown the possibility of controlling growth and development in a similar way and to a remarkable extent. The relation between the different members of a plant has also been exploited, largely within the past decade, although its beginnings were long ago. The study of correlations has cast much light upon the causes of form, and has made more impressive than ever the wonderful plasticity of plants.

Correlations. — Qualitative correlations, particularly, offer an inviting though difficult field for investigation. I need only mention a few examples of such correlations. Upon the removal of the terminal shoot of a pine, one or more of the lateral shoots erect themselves and undergo appropriate changes in mode of internal growth

and development, acquiring radial structure instead of dorsiventral, and branching on all sides instead of on the flanks. The transformation of sporophylls to foliage leaves following the removal of normal foliage has been a long-known example, to which renewed attention has been directed by the fine illustration of such change obtained in the experiments of Professor G F. Atkinson. It was shown by Knight nearly a century ago that the subterranean shoots of the potato, upon removal of the aerial parts, rise above ground and develop ordinary foliage leaves and flowers instead of tubers; while, conversely, the enclosing of aerial shoots in a dark chamber with saturated air gave occasion for the development of tubers, a phenomenon which is not uncommon under other than experimental conditions. A large number of similar transformations are now known.

Besides the accumulation of a greater range of such phenomena, we must look to the future for a luminous theory of this reciprocal influence of organs. At present there is little that is satisfactory in the discussion of the nature of correlation. In what conceivable way can the removal of one member act upon other parts so as to alter the course of its normal development? What can be the nature of the stimulus which overcomes the diageotropism of the horizontal subterranean branches of the potato, and induces upright growth and the development of foliage?

Regarding the quantitative correlations we are quite as much in the dark; perhaps more so, because of the relation of other functions. It is now clear that the greatly enlarged leaves and stems which develop after decapitation of a tree are in some way due to the increased food supply. But in what relation does the supply of food stand to these growths? Is the extensive removal of parts alone the stimulus which determines the revival of dormant buds and the formation of adventitious buds? Or does the increased amount of food act as the stimulus? But our present view of the movements of foods is that it is due to removal from solution, at the point where they are being used, of the substances which are needed. The using of food, indeed, is looked upon as both actuating and regulating, in large measure, the movement of food to any point. How, then, consonant with these ideas, can a superfluity of food occur at any point, there to act as a stimulus? Or how can excess of food in any way determine the increased *use* of food and so accelerate the growth of parts?

Pathology.—Closely connected with the study of the normal activities of plants are disturbances in the rate and character of function which are properly included under the term pathology. During the past decade very rapid advance has been made in a study of those pathological changes which are due to the presence of a foreign organism. Indeed, the phrase 'diseases of plants' calls to mind almost exclusively the effects of parasites, which cause wilting by mechanical stoppage of water supply, extraordinary growths in the form of tumors, destruction of chlorophyll to the detriment of photosynthesis, and a host of other evident changes. Indeed, as compared with other fields, we are tempted to say that this has been over-cultivated. The difficulty, however, is not so much in over-investigation as in over-publication regarding the distribution of the diseases and the application of palliatives and remedies. This is, in a measure, justified by the enormous economic value of the crops attacked. But one cannot help wishing that the staffs of our experiment stations particularly would give greater attention to investigations on the nature of diseased conditions than to repeating again and again the study of remedial operations.

There is thus one phase of pathology which has yet been comparatively neglected. The presence of a definite organism, whose activities clash with those of the host to the injury or death of the latter, is in itself an incitement to investigation. But we need also knowledge of those disturbed functions whose causes are dependent on other stimuli than the presence of a parasite. Some of these are doubtless internal and may long remain obscure, even as the causes of the so-called 'spontaneous' movements have hitherto eluded observation. But unquestionably many plant diseases are due to untoward conditions of the environment, working sometimes through chemical, sometimes through mechanical, sometimes through ethereal stimuli. This sort of work has been vigorously undertaken by the Division of Vegetable Physiology and Pathology at Washington, with full consciousness of the fact that, in order to attain results of value, there must be a fuller and more accurate knowledge of the normal processes.

At this point we are confronted by the difficulty of determining what processes are normal and what are pathological. It is the old question of sanity and insanity in a new guise—a question which each is tempted to answer in the same way as the old Quaker, who remarked to his wife: "Wife, they're all daft but thee and me; yea, and sometimes I think *thee* seems a little queer." What action shall be chosen as a norm is a matter of judgment, the general vigor of the plant alone serving as an imperfect criterion; imperfect, because we do not always know what constitutes vigor. Thus the study of pathology needs not only the examination of parasitic diseases, but also a wide acquaintance with the proper activities of healthy plants in order to determine what derangements are produced in them by untoward circumstances and obscurer internal causes. In the latter is an almost unworked field which promises rich reward for patient investigation, and that not only for the sake of pure science, but also for applied physiology as well.

If parasitic diseases cause among cultivated plants a loss of millions annually, is it unlikely that factors which can be controlled, if it is worth while to do it, cause in our crops a shortage whose money value may be many fold greater? There are already practical experiments tending to show that most of our field and garden crops steadily suffer for want of water, a want which windmills and water-driven electric pumps might often supply to great profit. We may not guess; we must *know* by experiments on a large scale whether or not it will pay to supply water and to control other unfavorable conditions, before we dare recommend such measures to a practical world.

IRRITABILITY.

I must now turn to a topic which is really deeply involved in all that I have already discussed, but one that deserves special mention. I mean the relation of irritability to the well being of plants. Seventeen years ago Sachs wrote: "Irritability is universal in the vegetable kingdom . . . Vegetable life without irritability is just as inconceivable as animal life without irritability. Irritability is the great distinguishing characteristic of living organisms; the dead organism is dead simply because it has lost its irritability."

It would be impossible to state the case more strongly. But it is one thing for him who has conceived a truth to state it clearly, and quite another thing to have this truth enter into the thinking and the experimenting of investigators. Long after the clear annunciation of the importance of irritability by the great physiologist—the father of modern plant physiology—too many were finding the chief rôle of irritability in those reactions which by deform-

ing the body moved the connected parts. Plant movements, especially those due to changes of turgor, were long looked upon as the main evidence of irritability in plants. This conception was reflected in the text-books of the older day and still survives in many of the more elementary works.

After the bearing of irritability on movements was firmly established, it came to be seen that the regulation of the rate of growth and its resumption by certain parts which had ceased to grow was accomplished through irritability. Growth, therefore, as well as movement, had important relations to irritability. But during the past decade, particularly, a better conception has been taking possession of physiological students. It is now perceived that *all* protoplasmic functions are initiated or controlled by external physical or chemical agents. This point of view is reflected in that masterly treatise of Pfeffer, the second edition of his *Pflanzen-physiologie.* Throughout the first volume, discussing the physical and chemical phenomena connected with metabolism, the ability of the protoplasm to regulate its own operations and to control even the physical changes in adjacent parts is everywhere presented and insisted upon.

The idea of a stimulus, instead of being confined, as it once was, to the action of heat, gravity and moisture, has now been greatly extended. Any external or internal change, slight or profound, gradual or sudden, which calls forth a corresponding change in the living protoplasm, is to be looked upon as a stimulus. The responses to stimuli, too, once thought of largely as those visible in curvature of motor organs or growing parts, are now conceived as of great variety. Invisible reactions probably outnumber the observable ones. Those producing a change of bodily form must be relatively few as compared with those which influence the performance of function or the course of development.

Diverse and numerous as are the stimuli which act upon plants, any conception of their operation would be faulty which fails to take into account the fact that stimuli of many unlike kinds and of unequal intensity are *interacting* to bring about the peculiar form and behavior of each individual plant. Think of the external agents which are known to be acting upon an ordinary land plant. About the aerial part the temperature varies from season to season, in our temperate zone changing from 30° below C. zero to 50° above; it varies from month to month and from day to day, even from hour to hour. The light differs in intensity and direction from day to night and from hour to hour. It changes in its actinic effect, as the photographer well knows, in the course of a few minutes; a variation, by the way, whose effect on plants has been entirely unstudied as yet. The moisture in the air is hardly the same for any two consecutive days; the plant is deluged with water for some hours or days and dry between rains; it is enveloped in fogs and mists; wet with dews at night, and all but blistered by the sun during the day. Its subterranean part is surrounded by solutions whose amounts and composition are probably varying hourly; whose concentration and consequent dissociation is changing from time to time. The temperature of the soil is scarcely the same from hour to hour; it varies between day and night, from day to day and from season to season. Imagine now the numberless combinations possible among these varying factors, and remember that all these interact as stimuli upon the protoplasm. What wonder, then, that no two plants are alike; that Capsella may flower at 5 cm. height with a few minute entire leaves, or may grow ten times higher with abundant foliage and long racemes of fruitful flowers!

This different conception of irritability and its relations to the functions of the

plant has led to many fruitful investigations during the past decade. The ingenious applications of plaster jackets for mechanical restraint of growth has thrown light not only upon the mechanical forces which can be exerted by growing organs, but casts a side light upon the difficult problem of the mechanics of growth. Researches upon the mechanics of curvature induced in growing organs by stimuli have been made by several observers, without obtaining, however, the concordant results which are to be desired. The subject, therefore, requires further study.

A satisfactory hypothesis as to what happens when an irritable organ is stimulated is still a desideratum. Is irritable protoplasm merely in a state of extraordinary lability, and does the stimulus initiate the decomposition of the protoplasm or of some unstable substance which it has produced? If this is true the metabolism of irritable organs which have been strongly stimulated ought to be different from that of similar but quiescent organs, and different products may be expected. One of the most noteworthy advances in this direction seems to be the discovery by Czapek (unfortunately we have had as yet only a preliminary paper) that roots after being geotropically stimulated contain notable amounts of reducing substances as compared with unstimulated roots which contain oxidizing substances instead.

Again, the transmission of impulses in plant tissues has been under frequent study. Haberlandt's seemingly well-founded conclusions regarding the transmission of impulses in Mimosa have proved untenable in the light of MacDougal's experiments, which also seem to shut out the possibility of the action of living protoplasm. The travelling of an impulse through a zone of dead cells is so marvellous that we are tempted to discredit the evidence of our senses, but that it occurs cannot be doubted. Thus, again, the discordant results of competent observers compel us to say that as good as nothing is now known.

ECOLOGY.

Within the past decade what may be considered a new division of plant physiology has been organized and has entered upon a development whose future extent and importance cannot yet be fully estimated.

Like every apparently new departure, it is an evolution from the old. Though its rise has been phenomenal, many of its facts and principles have long been known. At the meeting of the Madison Botanical Congress of 1893 the word *ecology* was almost new to American ears, and doubtless some present at that Congress were surprised at the introduction of a resolution on so unimportant a subject. The adoption of a name and preferable form of spelling for the new science, however, has been very useful in unifying the practice of American writers, and is a good illustration of the beneficial effect of a formal agreement on a matter of usage.

In the last century the relations of plants to insects were studied and Christian Conrad Sprengel's *Entdeckte Geheimniss der Natur* was a pioneer work in this subject. But Sprengel's work was destined to be forgotten for many years, and the further study of these interesting adaptations for the pollination of plants by insects was only revived by the prolonged observations and ingenious experiments of Charles Darwin. Since his time the work has been taken up vigorously and knowledge enormously extended by Müller, Ludwig, Delpino, McLeod, Robertson and a host of others.

The controlling influence of soil and climate upon the distribution of plants was also recognized and measurably understood long ago. In the classical works upon geographical distribution, such as Grise-

bach's *Vegetation der Erde* and Drude's *Pflanzengeographie*, the main features which form the basis for the grouping of plants are found to be those which constitute climate. Thus the moisture and heat relations of plants have dominated our thinking. The importance of these factors has particularly impressed itself upon students of local distribution. Again and again, in the past half century, local lists of plants have been compiled with little reference to the other conditions which determine the growth of plants. The limits of these local floras have been political boundaries, rather than the natural barriers to plant migration, or the physical features which determine climate. It has been the edge of the county, the boundary of the State, the limits of the country, which have been chiefly considered. In later years, however, the recognition of natural boundaries has become more common in these lists, and more attempts have been made to study the flora of a certain valley, a river system or a table land. Even so, however, natural barriers have been looked upon as controlling plant distribution merely through their effect upon climate, to the neglect of other factors.

In the last decade the increasing attention which has been given to the effect of external agents of all kinds upon plants, and the growing appreciation of the effect of stimuli upon plant form, acting through universal irritability, has led to the consideration of all the causes, small as well as great, which influence the well-being of plants. This knowledge, gradually accumulated, was first organized by Warming in his epoch-making work upon plant associations. Thus the subject of *ecology* was launched. The appearance of this great work not only brought into connection facts concerning the relations of plants to one another; it cast a new light upon the subject of plant geography. Facts and statistics which before had been dull and uninteresting to many, because without philosophy, now became luminous with new meaning.

This new light upon the geography of plants comes not merely from a consideration of the effect of the great factors of light, heat, moisture, and soil structure upon the plant; for these had been in a measure appreciated before. The new meaning arises from the introduction into the problem of the many minor factors of environment which act as stimuli and of the interminable variety of combinations which these present in their influence upon plant welfare. Among these environing conditions none is of greater importance than the effect of one plant upon another, partly direct and partly indirect, befriending some neighbors and injuring others. Because of these relations there arise groups of plants which grow well together, and others which are so antagonistic that they fly from one another's presence. These groundings may be due to causes the most remote or to relations the most intimate; according as they are due to one or the other will the association be closer or distant, the group large or small.

This phase of ecology, the study of plant societies, is yet in a somewhat chaotic condition. Not all the materials which are at hand have been satisfactorily organized, and much remains for future research. We await with impatience the settlement of various questions as to interpretation, and the acquisition of the multitude of new facts which are necessary before any true picture of the causes of form and the distribution of plant life is attainable.

It is a matter of some national pride that ecological investigations have been taken up vigorously by students in our own country, and that from the new standpoint some valuable researches on plant distribution have already been made. It is per-

haps also a matter of local pride that the most extensive study has been made in one of our great Western States, whose flora has been as yet comparatively little altered by the most potent of all disturbing factors, the hand of man. The *Phytogeography of Nebraska*, published a year or two ago by Pound and Clements, is the first extended study on plant geography in this country along distinctively ecological lines. The care and completeness with which their investigation was made render it a good example for future students of our flora, yet one which doubtless succeeding contributions will improve upon as the subject becomes better organized. As other examples of similar study may be mentioned the paper of Professor MacMillan upon the more restricted flora of the Lake of the Woods, and the only partially published work of Dr. Cowles upon the flora of the Lake Michigan dunes.

Plant names.—I venture to say that one of the most significant results of the study of ecology and physiological morphology is the growing dissatisfaction which its students feel with present methods of nomenclature, or perhaps I ought to say classification. I do not refer to the large grouping of plants into families, orders and divisions, but to the grouping of individual plants into species. This dissatisfaction is finding its expression among taxonomists as well. On the establishment of new species we are hearing almost daily the plea that it is better to separate into many species a group of nearly allied forms, although the differences used to distinguish them be very much slighter than those heretofore used for species. That is, it is better to do violence to our old idea of a species than to group together forms that in the field are easily recognized as unlike. This simply means that collectors and systematists are recognizing more fully the differences produced by unlike environment. It is a matter of common remark that the differences between individual plants recognized as belonging to one species are often greater than those which are used to separate species. Domesticated plants so easily pass into a variety of forms that for the sake of maintaining a rigid idea of specific rank cultivated plants have been quietly ignored. Now we are coming to see that in nature as in cultivation the plant is so plastic an organism that it is almost impossible to group together any individuals except those growing under identical conditions. What was devised as a convenience—namely, the establishment and naming of a species—is coming to be more and more of doubtful utility.

I will not undertake to say how much this species idea and nomenclature has retarded the true view of plant plasticity, but I feel sure that a good case might be made out for such a thesis. Whether any scheme can be devised which can replace the binomial nomenclature, whether any better method can be used by naturalists for designating the organisms which they are studying, is a matter for the future. I venture to prophesy, however, that the present system of nomenclature, by which I do not mean any particular kind of practice, whether of Paris, or Berlin, or Kew, or Cambridge, or Rochester, but the fundamental method of naming plants itself, *must go*. Our mere judgments, which we call species, foisted upon plants, do not conduce to a clear understanding of vegetable phenomena, but rather blind our eyes to a recognition of otherwise obvious truths. Some other method of identifying plants must be devised.

CYTOLOGY.

There is yet one other field whose development I must not fail to mention, though it does not pertain wholly to plant physiology. It goes without saying that the

functions of the plant body resolve themselves into the functions of the unit of that body. In every organ, however simple or however complex, we recognize the individual protoplast as the unit of work as well as the unit of structure. Each, enclosed in the armor-like wall which it has formed for itself, though hampered in its movements, is able to carry on the chemical and physical processes which constitute life without notable hindrance. Within the protoplast, for which Sachs uses the expressive though unnecessary word energid, there go on certain changes that can be observed with the microscope. These changes we look upon as the index of the invisible ones whose significance we seek to understand. It is natural, therefore, that the closest scrutiny should be made of the observable changes which take place within the cell. This minute study began in the attempt to ascertain how the living protoplasm constructed the wall with which it jackets itself. Every difference in composition which involved an optical alteration in the transmission of light, and so became visible, has been studied with the utmost care.

Later, attention was attracted to the division of the various independent protoplasmic organs within the cell body. Some of these have been found to be relatively simple. The division of the nucleus, however, has shown a complexity and at the same time a regularity which has challenged the minutest investigation and has made it the center of the greatest interest. So complex a series of changes, recurring with such regularity, argues an importance for both function and phylogeny which has made students eager to discover the secret. Therefore, within the last few years the behavior of the nucleus and of its different parts has been under study in all groups of plants with an exactitude never before dreamed of. Thus cytology has come to be an almost independent line of investigation. It is to be feared, however, that in many cases its exaltation has led students to mistake its real purpose and to consider it an end in itself. The visible processes within the cell will have little meaning unless they are looked upon as the mere index of its work. Unless the details of mitosis, for instance, are interpreted in the light of function or phylogeny they will certainly be misinterpreted or will be meaningless. It is becoming a question whether we have not overestimated the importance of slight differences in nuclear phenomena and whether further knowledge can be expected from a study of the visible processes within it. At the same time decided progress is to be hoped for in a more intimate chemical knowledge of the substances composing the nucleus, as to their chemical constitution and their relation to chemical reagents, such as stains and fixing fluids, rather than in repeated counting of chromosomes and multiplied observation of the details of prophase and anaphase.

I have now discussed the chief features of plant physiology in which notable progress has been making during the last decade. The great advances in plant chemics and physics; the progress in the investigation of causes of plant form; the widening ideas of the property of irritability; the investigation of the social relations of plants, and the minute study of cell action in spite of their diversity, have one great end in view. This is nothing less than the solution of the great problem—the fundamental problem—of plant physiology, as of animal physiology. The secret which we must discover, the dark recess toward which we must focus all the light that can be obtained from every source, is *the constitution of living matter*. Entrenched within the apparently impregnable fortress of molecular structure this secret

lies hid. The attacks upon it from the direction of physical chemistry and physiological morphology, of irritability, of ecology, and of cytology, are the concentrating attacks of various divisions of an army upon a citadel, some of whose outer defences have already been captured. The innumerable observations are devised along parallel lines of approach, and each division of the army is creeping closer and closer to the inner defences, which yet resist all attacks and hide the long-sought truth. We see yet no breach in the citadel. Here and there we seem to approach more closely and at certain points are getting glimpses, through this loophole or that, of inner truths, hidden before.

One outer circle of defences yet remains untaken, and until that falls it would seem that there is little hope of capturing the inner citadel. We *must* know more of the constitution of dead substances chemically related to the living ones. When the students of chemistry can put the physiologists into possession of the facts regarding dead proteids we shall renew the attacks more directly, with greater vigor and greater hope of success.

That ultimate success is to crown our efforts there is little reason to doubt. Ten years ago we little dreamed of the tremendous strides as since made toward the interpreting of life's central truth. The success of the past is the best augury for the future. The brilliant researches upon the chemistry of carbon compounds inspire us with renewed hope and put into our hands almost daily new weapons.

It is not possible to prove to-day that life and death are only a difference in the chemical and physical behavior of certain compounds. It is safe to say that the future is likely to justify such an assertion. In the meanwhile we press forward along the whole line. Botany is more than ever full of meaning, because with its sister sciences it is no longer seeking things, but the reasons for things. CHARLES R. BARNES.

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SECTION A—ASTRONOMY AND MATHEMATICS.

THE address of Vice-President Alexander Macfarlane entitled 'The Fundamental Principles of Algebra,' and the 'Report on Progress in Non-Euclidean Geometry,' by Professor George Bruce Halsted, of the University of Texas, are both to be published in full in SCIENCE and will not be treated further here.

A Report on the Recent Progress in the Theory of Linear Groups, presented by Professor L. E. Dickson, of the University of California, was of the nature of a supplement to the report on finite groups, read at the last annual meeting of the Association, by Dr. G. A. Miller, of Cornell. It is intended for publication in the *Bulletin of the American Mathematical Society*, in which the report of Dr. Miller appeared last year.

Part I. of the present report gives the general theorems relating to the canonical form of finite groups of linear substitution and to the generators of such groups. After a complete enumeration of the binary and ternary collineations in their historical setting, a number of special quaternary linear groups, particularly the famous one of order 51,840, are considered.

Part II. treats of linear groups in a Galois field, their order, generators, factors of composition and the isomorphisms existing between them. The Galois field is defined and a full bibliography added. The general linear homogeneous group, the linear fractional group, the Abelian linear group and its generalized form, the first and second hypoabelian groups, the orthogonal group, other linear groups with a quadratic invariant or a special invariant of degree q, the hyperorthogonal group and the hyperabelian group are all treated in turn. A number of